I found the mouth parts to be a perfect mine of stings. In all fifty were extracted, more than forty of which were imbedded in the flesh adherent to the jaw cartilages. These stings varied in size from perfect specimens four or five inches in length to broken-off tips hardly more than one inch long. These broken-off stings were especially abundant at the angles of the jaws where as many as three or four tips were frequently found in a cube of flesh one inch square and two inches long. One can only conjecture how many could have been found by a careful dissection of the flesh of the mouth and throat. The dissection of the jaws was not gotten at until about forty hours after the capture of the shark and its condition consequently was such as to prevent the minute dissection necessary to extract all the spines in the throat region. The lower jaw cartilages were scarred and ridged from angle to symphysis, evidently by stings received in former combats. Some of the stings were manifestly but newly implanted, for the flesh around them was still red from congested blood, in other cases the redness had all disappeared, while some of the stings were plainly old, being imbedded in cysts. Especially was this latter condition true of those piercing the membrane surrounding the cartilages.

Not knowing that anything has been discovered as to the especial food of the hammerhead shark, I wish to advance the suggestion that this is to a certain degree made up of its not far distant kinsman, the sting-ray. This suggestion is based on three facts. First, that this shark was chasing sting-rays when harpooned, and was so eager in the chase that, when the first 'iron' pulled out, it kept up the chase in the neighborhood of the boat until harpooned a second time. Secondly, on the finding of the skeletal remains of rays in its stomach. The whole skeleton of a long-tailed ray found there seems to prove that the remains were not those of the butterfly ray (*Pteroplatea maclura*), which is abundant at Beaufort, but of *Dasyatis say*, the most common armed form. Thirdly, the very large number of stings found in and around the mouth parts indicates the number of rays which this shark caught and which had been successful in stinging it.

Since writing the above paragraph, my attention has been called by Dr. Theodore Gill to a note by Dr. Edwin Linton in which the latter states that from dissections of fifteen small specimens of another species of the same genus of shark, *Sphyrna tiburo*, at Beaufort, he found that the food consisted chiefly of Crustacea—blue crabs, *Mantis* and other shrimps, and acorn barnacles—of seaweed, and of pieces of fish used for bait; but not of whole fish such as they might be expected to prey upon.[1]

E. W. GUDGER

STATE NORMAL COLLEGE,
GREENSBORO, N. C.,
January 24, 1907

DO OFFSPRING INHERIT EQUALLY FROM EACH PARENT?

THE alleged fact that offspring inherit equally from each parent, together with the striking parity, in number, size and form, between the chromosomes of the mature male and female germ cells, notwithstanding the great disproportion in size between the egg and the spermatozoon themselves, is frequently advanced as one of the strongest supports of the chromosome theory of inheritance.

But do we inherit equally from each parent? What seems obvious at first glance becomes very doubtful upon closer inspection. The vast majority of the characters of a given organism, such, for example, as make it an animal and a vertebrate of a given genus and species, are obviously characters which are common to both parents. The only characters which we can measure are the minor ones of individual or specific peculiarity, and while these, apparently, may be derived equally from either parent, this conclusion is very different from one which would affirm that the qualities of the offspring as a whole are derived equally from each parent. The hybridist can

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[1] These observations were made while I was acting as a temporary assistant in the Fisheries Laboratory at Beaufort. For permission to publish them here, I wish to thank the Commissioner, Hon. George M. Bowers.

help us little here, because his so-called 'unit characters' are only these same superficial individual and specific qualities, and the fact that the crossing of any but comparatively closely related forms is impossible, precludes any final solution along this line.

The facts at our command, indeed, indicate that the female germ cell determines the fundamental animal form together with its more constant characters. Driesch, for example, found that in hybrid echinoderms, no matter from what species the sperm were taken, the manner and rate of cleavage, the character of the mesenchyme formation and of gastrulation always followed the *maternal* type. Standfuss has shown that young butterfly hybrids first resemble the maternal species, but diverge more and more towards the male species with each metamorphosis, as individual qualities begin to assert themselves, until the hybrid comes to its ultimate degree of intermediacy.

If we accept the idea of 'formative substances' as advanced by Conklin or Lillie, whether we regard these substances as really specific organ-forming materials or as indicating corresponding cytoplasmic localizations, then the fundamental organology is already laid down in the egg before the spermatozoon enters, and the egg passes on to cleavage without waiting for an equal amount of 'formative substance' to pass out from the male pronucleus and take joint possession of the already localized areas. For example, Lillie[1] states that at fertilization the presence of the sperm involves no important changes in the topography of the several formative substances which are distributed throughout the cytoplasm of the egg. Since, then, there is no evidence of such a biparental mechanism in early stages, is it not decidedly far fetched to postulate one, especially when the single one that already exists is adequate?

If it is true that offspring do not inherit equally from each, but more from the maternal parent, then the argument for the morphogenetic nature of chromatin based upon the striking parity between the chromosomes of male and female germ cells after reduction loses its force, if we still cling to the idea that the chromosomes are the *exclusive* bearers of hereditary qualities.

Contrary to the view that fertilization is primarily concerned with the mingling of hereditary qualities, many zoologists have come to regard it as satisfying some periodic physiological need of the organism, and while one conception is perhaps as hazy as the other, still the latter opens up an equal possibility that the reduction divisions have to do with maintaining a metabolic equilibrium of some kind, instead of acting as a mechanism for the casting out of heritable morphological units.

But granted that the chromosomes are the bearers of specific morphogenetic substances, even then the facts (1) that there is apparently a persistence of the individuality of the chromosomes through successive cell-generations, and (2) that the final behavior of the chromosomes in reduction division is in seeming accordance with the demand of the Mendelian principles—even these facts do not necessarily restrict us to a purely chromosomal hypothesis of heredity nor to the idea that offspring inherit equally from each parent. However, since this is one of the most significant lines of argument for this hypothesis, it merits more detailed discussion.

Various hybridists, judging from the external visible characters of hybrids, came to the conclusion that in the germ cells of hybrids there must be a separation of parental qualities so that with respect to a given quality, half of the germ cells returned to the maternal, half to the paternal types. Conversely, I had in the meantime, from studying the germ cells of hybrid doves and pigeons, called attention to the fact that there is apparently a segregation of maternal and paternal chromosomes at the reduction period which, if the chromosomes bore hereditary qualities, would lead to the establishment of pure germ cells, and thus afford a possible explanation of how the offspring of hybrids come to show returns to grandparent types.[2]

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[1] *Jour. of Exp. Zool.*, III., 2, p. 178.

[2] SCIENCE, February 16, 1900.

However, I had previously noted and recorded[3] this fact of the reversion of the offspring of hybrids to the grandparent types.

Later Montgomery (1901) and Sutton (1902), working on non-hybrid forms, which have chromosomes of varying size, presented striking evidence of the fact that in early germ cells there are pairs of homologous chromosomes, one of paternal and one of maternal origin, and that these homologous chromosomes unite in synapsis. The ensuing reduction division simply brings about their separation and segregation in different cells.

Although I had elaborated the idea of the relation between the chromosomal phenomena of hybrids and the reversion of their progeny, in my doctoral thesis of 1900, the published statement of the details did not come out until November, 1902,[4] but these details show that I had hit upon practically the Mendelian idea. Very soon after the appearance of my paper in 1902, Cannon, Wilson and Sutton published conclusions of a very similar nature, endeavoring to offer a cytological interpretation of the Mendelian principles, which had had their renaissance in the meantime. Only Cannon's conclusions, however, were based upon the actual study of hybrid material. In this way it became established that there is a mechanism in germ cells which, assuming that the chromosomes are concerned in heredity, could possibly lead to a segregation of paternal and maternal qualities.

But if we accept the idea of Boveri and of Sutton that each chromosome contains only a certain pro rata of adult characters, and that reduction is simply the separation of homologous mates, then besides facing the unproven though necessary implication that whole blocks of grandparental characters are barred from the third generation, we must also recognize, as pointed out by Davenport and others, that this theory is not in harmony with certain facts of non-alternative (non-Mendelian) inheritance. How, for example, are we to account for the well-authenticated instances of (1) blended inheritance, (2) of pronounced atavism, such as is seen in mongrelized breeds of pigeons, which tend to return to the primitive ancestral blue-rock type with apparently none of the components missing, (3) of exclusive inheritance or prepotency, (4) of the later outcropping of dominant characters in a recessive individual, which has sprung from a gamete that, according to this chromosomal theory, has been purged of such dominants, or, in other words, the contamination of a given character by its allelomorph, and (5) of the 'fixation' of a hybrid mosaic gamete, of which the qualities do not segregate in subsequent generations?

Even though we have visible evidence of the separation of homologous chromosomes, I fail to see why this necessarily means that each has retained all of its original qualities, or has taken on no new ones. It is easily possible that there can be persistence of form in these chromosomes without persistence of qualities. Supposing that the chromosomes differ from one another in their physical properties (and they doubtless do, more or less, since we can recognize constant types), the form might easily be dependent upon the physical consistency of each of the particular chromosomes, which, in fact, is made up of at least two substances, viz., chromatin and linin. It is evident that in pro-synaptic stages when the chromosomes are characteristically present as hazy granular masses, numerous conjugations or exchanges of individual granules could occur, and yet the matrix (linin) bearing the qualities, persist and appear finally in its characteristic form.

In my own study on the spermatogenesis of hybrids, I was finally led to consider the strict individuality of the chromosome as persisting only in hybrids derived from widely divergent forms. In the case of fertile hybrids my idea was expressed as follows: "The cases in which the entire plasmas are segregated are then probably but magnified images of what occurs among the specific qualities of the milder crosses."[5] Furthermore, I have suggested that the occasional inequalities in the divisions of individual chromosomes might

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[3] *Zoological Bulletin*, Vol. II., No. 5, 1899.

[4] 'Hybridism and the Germ-cell,' *University of Cincinnati Bulletin*, No. 21, November, 1902.

[5] *Cincinnati Lancet-Clinic*, May 9, 1903.

account, in part at least, for the fact that all germ cells are not absolutely pure in hybrids, and it may be thus that in cases of apparently complete return to one parent type, characteristics of the other parent may, nevertheless, crop out from time to time in succeeding generations.[6]

In the foregoing attempt to reconcile the behavior of chromosomes with the Mendelian principles it is clearly assumed that the chromosomes are the mechanism, or at least the chief mechanism of heredity. But turn them and juggle them as we may, we see that it is difficult to make the conclusions of the cytologist who clings to an exclusively chromosomal theory fit into the facts of heredity, and the difficulty becomes all the greater if it is true that the male and the female do not contribute equally in heredity. The latter difficulty, together with an attempt to explain reversions, led me to the suggestion, in a former paper, that both cytoplasm and nucleus are involved specifically in inheritance, the cytoplasm of the germ cell representing the more stable and constant form of the animal, and the chromatin the more individual and variable characteristics. If the male contributes chiefly individual qualities, and if we accept these as being borne in the chromosomes, then since these chromosomes are so strikingly paralleled by those of the female in both number and form, we might infer that the chromosomes of the female likewise bear only individual and variable qualities, while the cytoplasm bears the fundamental qualities.

The material starting points (or *inceptors*) of definite characters were conceived of as arising through the activity of chromosomal emanations on cytoplasmic materials at different stages in the development of the organism. Since the chromatin was looked upon as the more variable cell constituent, it, rather than the cytoplasm, was regarded as conditioning the more variable characteristics, without, however, precluding some nuclear activity at all stages of development. There is every reason to believe that both cytoplasm and nucleus in a given species are *distinctive* of that species and there is no conceivable reason why the cytoplasm any more than the nucleus must be made so anew in each generation. The variable nature of chromosomes is evidenced in the pronounced irregularities which are induced in them through hybridizing or drugging. Furthermore, the intimate mingling of the chromatin from the two sexes, the known fact that definite substances (enzymes, etc.) emanate from the nucleus, and the highly unstable nature of nucleo-proteids, would point to the chromosomes as, at least, an adequate source of variability. Lastly, the facts of differentiation, before fertilization, etc., mentioned above, seem to indicate that offspring do not inherit all characters equally from parents but rather only the more superficial ones, and that, therefore, chromosomes, which are derived equally from each parent, are connected in some way with such superficial characters.

Furthermore, such an interpretation would harmonize better with the fact that the numerical variation of chromosomes in closely related groups may be out of all proportion to the character differences of the groups. For example, Miss McGill, working on *Anax,* has found 28 chromosomes, while in some recent studies on a *Libellula* I find 23 or at most not over 24 chromosomes. How, then, on the exclusively chromosomal hypothesis of heredity, are we to account for the discrepancy in the number of chromosomes, such as exists between two members of so restricted a group as the Odonata, which, despite their individual differences, must have the vast majority of their fundamental features in common? Or how account for the pronounced numerical differences in chromosomes as recorded by Wilson in different genera of the Heteroptera. For example, *Anasa tristis* has 21 in the male and 22 in the female, while *Protenor belfragei,* or *Alydus pilosulus,* has 13 in the male and 14 in the female. Even related species of the same genus may differ in the number of chromosomes, and there are indications that this may be true of different individuals of the same species. The numerical differences would

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[6] See 'Spermatogenesis of Normal and of Hybrid Pigeons,' p. 48.

seem to be out of all proportion to the actual differences between the adult genera or species.

The facts would seem to force us, if we still cling to the idea that in chromosomes we are to find specific morphogenic substances, to some such postulate as the one already suggested, that only the more superficial and fluctuating qualities are borne in the chromosomes, for then we might appreciate how considerable fluctuation in the number of chromosomes in different species might be reconcilable with the relatively smaller differences between the adults.

However, this idea of the respective rôles of cytoplasm and nucleus in inheritance was offered only as a suggestion, and not as a theory and such it must remain, unless some more convincing evidence is forthcoming. Its only value in this connection is to show that we are not restricted to a consideration of the chromosomes as the sole vehicle of heredity, and that equality in the amount of chromatin contributed by each parent, even should we succeed in assigning heritable qualities to the chromosomes, does not necessarily imply that we inherit equally from each parent.

Michael F. Guyer
University of Cincinnati,
March 12, 1907

THRUSTS AND RECUMBENT FOLDS, A SUGGESTION BEARING ON ALPINE STRUCTURE[1]

Let it be assumed that as a result of a shearing strain a thrust fault, *A*, is initiated in the crystalline basement of a sedimentary series, and that displacement occurs along a plane which rises at a gentle angle to the plane of stratification. Let it be assumed further that the strata comprise a soft shale overlain by a limestone of moderate thickness, above which is a thick series of sediments.

The immediate effect on the shale will be to thicken it in front of the overthrust crystallines (as was repeatedly observed in the case of soft layers under similar conditions of pressure in experiments on folding described in the Thirteenth Annual Report of the U. S. Geological Survey). In swelling the shale will have somewhat the effect of a laccolithic intrusion and will raise the overlying limestone, forming an anticline.

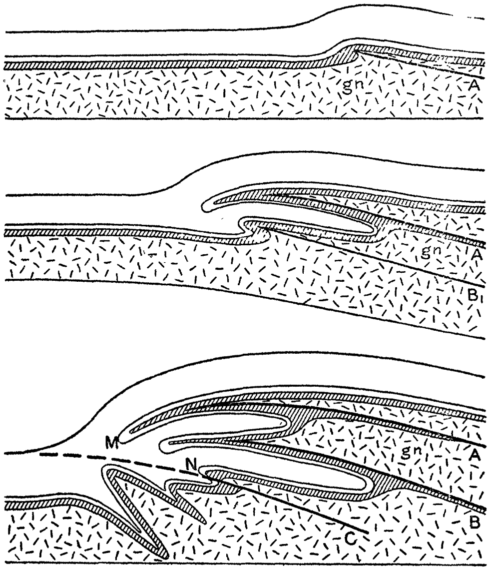

Fig. 1. Hypothetical Development of Recumbent Folds from Overthrust Faults.

If the plane of the thrust forms an acute angle with that of the bedding, the shear may follow the bed of shale, thus separating the limestone and overlying strata from the underlying; and the stress transmitted by the advancing tongue of gneiss to the limestone may roll the latter back upon itself. The overlying strata would become more or less involved in the overfold.

The recumbent fold will develop to a length determined (1) by the competency of the strata to transmit thrust; (2) by the effect of the resistance, which increases as the strata pile up; and (3) by the conditions favoring the development of a second thrust fault, *B*.

If the movement continues to the production of a second thrust, *B*, the plane of the thrust, *A*, and the recumbent beds will be raised into an anticlinal attitude, as the flat strata were in the first instance. Thus the point of the overturn, *M*, will appear to be bent downward, and if movement continues on the thrust, *A*, it may become bent under. Such movement could not, however, continue

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[1] Read before the Geological Society of Washington, April 10, 1907.